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CHAPTER 7

The Relative "Importance" of Life-History Stages to Population Growth: Prospective and Retrospective Analyses

Carol Horvitz, Douglas W. Schemske, and Hal Caswell

Determining the importance of life-history events for population growth is a significant, if ill-defined, goal of population-dynamics research. Perturbation analyses, which explore the effects on population growth of changes in the vital rates, provide an approach to this problem. They have become a standard part of demographic practice. It is now rare to find a published report of population growth rate that does not investigate how that rate changes as the vital rates are perturbed, either actually (comparing different treatments, sites, species, etc.) or hypothetically (exploring the consequences of potential management strategies or of evolutionary changes). Applications include life-history theory (where it is important to know how the different vital rates influence fitness; see, e.g., Caswell & Werner 1978; Caswell 1985; Calvo & Horvitz 1990; Kalisz & McPeek 1992; Calvo 1993), conservation biology (where it is important to know how protecting different stages in the life cycle would affect population growth; see, e.g., Crouse et al. 1987; Menges 1990; Doak et al. 1994; Heppell et al. 1994; Schemske et al. 1994), ecotoxicology (where it is important to know how pollutants affect population growth; see, e.g., Caswell 1996*a*; Sibly 1996; Levin et al., in press), and assessing the accuracy of estimates of population growth rate (Lande 1988).

Unfortunately, as the use of demographic perturbation analyses has spread, so have some common misconceptions about them. Our goal in this chapter is to clarify some of the applications and interpretations of perturbation analyses. Much of the confusion stems from apparently reasonable but ambiguous questions, perhaps the most ill posed of which is, "which of the stages, or which of the vital rates, is most important to population growth?" The problem is that "importance" has several different meanings, each of which leads to a different perspective on the population.

It is useful to distinguish between *prospective* and *retrospective* answers to this question. Prospective analyses address the effects of potential future changes. Of all the changes in the vital rates, which would produce the biggest effect on population growth rate? No changes in any vital rates need have occurred to ask this question. It is even possible, and sometimes instructive, to ask about changes that are purely hypothetical ("if pigs had wings ..." or "if this species were to become a perennial instead of an annual ..."). Sensitivity and elasticity analyses (see Chapter 2 and Caswell 1978; Caswell et al. 1984; de Kroon et al. 1986) are prospective analyses.

A common misconception about prospective analyses is that a high sensitivity or elasticity for some parameter implies that an observed change in population growth rate was due to that parameter. This is a mistake; analyzing changes in population growth that have actually occurred is a retrospective, not a prospective, problem. Some change in the vital rates has actually occurred, leading to the change in population growth rate. We want to know how much of the change in population growth rate can be attributed to the changes in each of the vital rates. The vital rate that contributes the most to the variability in population growth is not necessarily the one to which population growth rate is most sensitive, nor the one that will make the biggest contribution to variability in population growth rate in another environment. Some vital rates to which population growth is very sensitive may never vary, and thus make no contribution to the variability.

The appropriate analytical tool for this question is the "decomposition analysis" of life-table-response experiments (Caswell 1989*a*, 1996*a*). If population growth rate is measured as a deviation from a reference value (e.g., a treatment relative to a control), then the treatment effect can be decomposed into contributions from each of the vital rates. If variability in population growth rate is expressed as a variance over a set of treatments, this variance can be decomposed into contributions from the variances and covariances of the vital rates.

Confusion about retrospective and prospective perturbation is analogous to some common misinterpretations of genetic-heritability analysis (Lewontin 1974). Heritability decomposes an observed phenotypic variance into genetic and environmental contributions. It is a retrospective calculation. High heritability does not mean that the trait is insensitive to the environment; that is a prospective conclusion. The trait might be, for example, sensitive to temperature, but the data were collected in a constant-temperature chamber. Similarly, low heritability does not mean that the trait is insensitive to changes in genetics. Perhaps the trait is affected by genotype, but the population studied was homozygous at the relevant loci.

We describe five analyses, two prospective and three retrospective, that address the question of how the vital rates affect population growth rate. Then we apply them to data on the Neotropical understory herb *Calathea ovandensis*. Comparison of the results sheds light on various aspects of the "importance" of the vital rates in this particularly well studied case.

1 Demographic Analyses

We use the linear time-invariant matrix model

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)\,, \tag{1}$$

where $\mathbf{n}(t)$ is a vector giving the abundances of the stages in the population at time t, and $\mathbf{A}$ is the population-projection matrix, whose ijth entry a_{ij} gives the contribution of an individual in stage j to stage i over one time step. See Caswell (Chapter 2, or 1989*a*) for details. The dominant eigenvalue λ of the matrix gives the population growth rate. The associated right and left eigenvectors $\mathbf{w}$ and $\mathbf{v}$ give the stable stage distribution and the stage-specific reproductive values, respectively.

Sensitivity and elasticity formulas are derived in Chapter 2. The sensitivity of λ to a change in the matrix entry a_{ij} is given by

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}\,, \tag{2}$$

where $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of $\mathbf{w}$ and $\mathbf{v}$. The elasticity, or proportional sensitivity, of λ to a change in a_{ij} is given by

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}\,. \tag{3}$$

It is sometimes suggested that sensitivity or elasticity analysis

is better, or more accurate, or less biased, or more biologically reasonable than the other. This is not so. The two give different pictures of the result of a perturbation. The pictures are each accurate, unbiased, and biologically meaningful. Population growth rate (λ) is a function of the entries of the population-projection matrix. Imagine plotting λ as a function of one matrix, say a_{ij}, while holding the other entries constant. Plot a_{ij} on the x-axis and λ on the y-axis. The slope of the resulting curve is the sensitivity of λ to changes in a_{ij}. If you were to repeat this operation for all the matrix entries, the result would be a set of curves with different slopes; those slopes would show how λ responds to changes in all the matrix entries. Alternatively, imagine plotting λ as a surface in a multidimensional space, as a function of all the a_{ij}. The sensitivities s_{ij} give the gradient of this surface, showing in which directions it slopes steeply and in which directions it is relatively flat. This is the key to the evolutionary applications of sensitivities, which can be interpreted as selection gradients (Lande & Arnold 1983; Phillips & Arnold 1989).

Now, imagine the same exercise, but plot the logarithm of λ as a function of the logarithm of a_{ij}. The slope of this line is the elasticity of λ to changes in a_{ij}. The multidimensional analogue is the gradient of a surface that shows $\log \lambda$ as a function of the logarithm of the matrix entries. The elasticity $e_{ij} = 0$ if $a_{ij} = 0$. That is, if the wingspan of a pig increases by, say, 10 percent, there is no change in its flying ability. Transitions directly from newborn to large reproductive individuals (entries in the lower left corner of the matrix) usually have high sensitivities, even though such transitions may not occur. The sensitivity indicates correctly what *would* happen if that rate were increased from zero to a small positive number. The elasticity, however, is zero and can reveal nothing about such changes. This makes elasticity inappropriate for evolutionary questions such as asking how fitness would change if an annual were to become perennial, or seed dormancy were to be introduced where it does not exist, etc. The elasticity, in contrast, indicates correctly that increasing the matrix entry by some proportion has no effect on λ.

The elasticities sum to 1 across the whole matrix (Caswell 1986; de Kroon et al. 1986; Mesterton-Gibbons 1993) and can be interpreted as proportional contributions of the corresponding vital rates to λ (see van Groenendael et al. 1994). There is some confusion between the correct statement "stage x contributes y percent to population growth rate" and the incorrect statement "stage x

explains y percent of the *variation* in population growth rate," which cannot be determined from an elasticity analysis.

Is elasticity more meaningful than sensitivity? The choice of arithmetic or logarithmic axes is a matter not of right or wrong but of which graph reveals the aspects of the curve that are of interest. Logarithmic axes are useful because equal intervals correspond to equal proportions. If you are interested in patterns involving proportional changes in vital rates, use the slopes of the logarithmic plots (i.e., the elasticities). Equal intervals on arithmetic axes imply equal changes. If you are interested in rates of change on a linear scale (as evolutionary questions are, for example), then use sensitivities. Better yet, make both calculations and compare the results.

Remember that both sensitivity and elasticity are derivatives; they give the local slope of λ (or $\log \lambda$) as a function of a_{ij} (or $\log a_{ij}$). They may not accurately predict the result of large perturbations (although, in practice, they do a surprisingly good job). Using the second derivatives (Caswell 1996*b*) to take into account the curvature of λ might improve the prediction. A more straightforward approach, however, is to vary parameters and calculate λ numerically (see, e.g., Caswell & Werner 1978; Bierzychudek 1982; Horvitz & Schemske 1986; Martinez & Alvarez-Bullya 1986; Calvo 1993). For example, an effective but rare pollinator may increase plant reproductive success several-fold. A local-perturbation analysis near the usual low level of fruit production may not accurately predict the effect of the pollinator on λ, while a simulation that actually varies fruit set and calculates λ will do so (Horvitz & Schemske, unpubl. data). Numerical perturbation analysis is also useful for investigating specific, biologically interpretable changes in several of the vital rates simultaneously. It should, however, be supplemented with analytical results.

2 Retrospective Analysis

A retrospective analysis begins with data on the vital rates and on λ, under two or more sets of environmental conditions. The goal of the analysis is to quantify the contribution of each of the vital rates to the variability in λ. A formal method for quantifying data of this kind has been called Life-Table-Response Experiments (LTRE's) (Caswell 1989*a*, *b*, 1996*a*, in press; see also Levin et al. 1987, in press; Walls et al. 1991; Brault & Caswell 1993). This usage defines "experiment" in a sense wide enough to include not

only designed manipulations but also comparative observations.

Intuitively, variation in one matrix entry, say a_{ij}, makes a small contribution to the variation in λ if a_{ij} doesn't change much, or if λ is not very sensitive to a_{ij}, or if both are true. Thus, the contribution of a_{ij} to the variation in λ involves the product of s_{ij} and the observed variation in a_{ij}.

As in the familiar analysis of variance, LTRE analysis depends on whether the "treatments" are considered a random sample from some universe of possible conditions or a fixed set of treatments that are of interest in themselves and could be repeated if necessary. As in statistics, the distinction between random and fixed treatments is subtle, and one data set may well be interpreted differently by different people. In a random design, the results are characterized by the variance of λ, and the goal of the analysis is to decompose this variance into contributions from the variances of (and covariances among) the matrix entries (Brault & Caswell 1993; Caswell & P. Dixon, unpubl.). In a fixed design, the results are described in terms of the effect of each treatment on λ, measured relative to some baseline. The goal of the analysis is to decompose the treatment effects into contributions from the treatment effects on each of the vital rates. (There are also LTRE methods for quantitative treatments, analogous to regression models; see Caswell 1996*a*; Caswell & L.V. Martin, unpubl.)

Random Treatments: Variance Decomposition

Let $V(\lambda)$ denote the variance of λ among treatments. Recall the formula for the variance of a linear combination of two random variables x and y:

$$V(ax + by) = a^2V(x) + b^2V(y) + 2abC(x, y), \tag{4}$$

where $C(x, y)$ is the covariance of x and y. Approximating λ as a linear function of the a_{ij}, and using the sensitivities s_{ij} as the slopes, yields

$$V(\lambda) \approx \sum_{ij} \sum_{k\ell} C(ij, k\ell) s_{ij} s_{k\ell}, \tag{5}$$

where $C(ij, k\ell)$ is the covariance of a_{ij} and $a_{k\ell}$, and the sensitivities are calculated at the mean matrix. The covariances are calculated directly from the data on $\mathbf{A}$ for each environment. Each term in this summation is the contribution of one pair of vital rates to $V(\lambda)$. This calculation was first used to examine the variation in λ among pods of killer whales (Brault & Caswell 1993).

Because $V(\lambda)$ depends on the covariances among pairs of vital rates, it is difficult to say which rate, as opposed to which pair of rates, makes the biggest contribution. One way to define the contribution of a single rate is to sum the contributions for all the covariances involving that rate:

$$\chi_{ij} = \sum_{k\ell} C(ij, k\ell) s_{ij} s_{k\ell}. \tag{6}$$

This sum includes the contribution to $V(\lambda)$ from the variance of a_{ij} plus half the contributions from the covariances of a_{ij} with the other rates. The other half of the covariance contributions is distributed among the contributions of the other matrix entries. We call this calculation of the contribution χ_{ij} the "covariance method."

A special case: independent variation. If it seems safe to assume that the vital rates vary independently, then the approximation for the variance reduces to

$$V(\lambda) \approx \sum_{ij} V(a_{ij}) s_{ij}^2, \tag{7}$$

where $V(a_{ij})$ is the observed variance in the ijth element of the matrix $\mathbf{A}$. Each term in this summation represents a contribution of one vital rate to $V(\lambda)$; by definition,

$$\chi_{ij}^{\text{ind}} = V(a_{ij}) s_{ij}^2 . \tag{8}$$

As with the covariances in the preceding case, the variances here are calculated from the observed set of matrices and the sensitivities are calculated at the mean matrix. We call this the "variance method" of calculating the contribution χ_{ij} to $V(\lambda)$.

Choice of a reference matrix. The variance $V(\lambda)$ is the average of the squared deviations from the mean of the growth rates, and thus the sensitivities in the approximations (6) and (8) are calculated from the mean matrix. However, other matrices might serve as more-reasonable reference matrices. In the data set we analyze next, we use a summary matrix computed from the pooled data from all sites and years. This is equivalent to using a weighted mean with weights proportional to the sample sizes. In this case, $V(\lambda)$ is no longer strictly speaking a variance; it is the mean-squared deviation from the reference matrix, and $C(ij, k\ell)$ is no longer a covariance; it is the mean of the cross-product of the deviations of a_{ij} and $a_{k\ell}$ from their values in the reference matrix.

Fixed Treatments: Decomposing Treatment Effects

A fixed-effect analysis treats the matrices as representative of particular conditions, either experimental or natural (high vs. low nutrients in a one-way model, for example, or year and spatial location in a two-way model). The goal is to determine how much of the main effect of each treatment level on λ is contributed by each of the vital rates. In a factorial design, this can be extended to include the interaction effects of combinations of factors as well as the main effects.

The analysis uses a linear approximation in which the sensitivities appear as slopes. The effect of a treatment on λ depends on its effect on each matrix entry and on the sensitivity of λ to that entry.

In order to analyze a data set in which plots and years appear as fixed effects, we write a two-way model (as in an analysis of variance) for population growth in plot m and year n:

$$\lambda^{(mn)} = \lambda^{(\cdot\cdot)} + \alpha_m + \beta_n + (\alpha\beta)_{mn}\,, \tag{9}$$

where $\lambda^{(\cdot\cdot)}$ is the growth rate calculated from $\mathbf{A}^{(\cdot\cdot)}$, the grand mean of all the matrices, and α_m, β_n, and $(\alpha\beta)_{mn}$ are the plot, year, and interaction effects. These effects are estimated by

$$\alpha_m = \lambda^{(m\cdot)} - \lambda^{(\cdot\cdot)}\,, \tag{10}$$

$$\beta_n = \lambda^{(\cdot n)} - \lambda^{(\cdot\cdot)}\,, \tag{11}$$

$$(\alpha\beta)_{mn} = \lambda^{(mn)} - \alpha_m - \beta_n - \lambda^{(\cdot\cdot)}\,. \tag{12}$$

Here, the growth rates $\lambda^{(m\cdot)}$ and $\lambda^{(\cdot n)}$ are the growth rates calculated from the mean over years of the matrices for plot m and from the mean over plots of the matrices for year n, respectively.

These treatment effects on λ can be decomposed into contributions from the effects on each matrix element, as follows:

$$\alpha_m \approx \sum_{ij} (a_{ij}^{(m\cdot)} - a_{ij}^{(\cdot\cdot)}) s_{ij}\,, \tag{13}$$

$$\beta_n \approx \sum_{ij} (a_{ij}^{(\cdot n)} - a_{ij}^{(\cdot\cdot)}) s_{ij}\,, \tag{14}$$

$$(\alpha\beta)_{mn} \approx \sum_{ij} (a_{ij}^{(mn)} - a_{ij}^{(\cdot\cdot)}) s_{ij} \tag{15}$$

(Caswell 1989*a*,*b*). Because the sensitivity structure may change from one treatment to another, the sensitivity matrix is evaluated

at a matrix that is intermediate between the treatment being considered and its reference matrix. For α_m, this intermediate matrix is $(\mathbf{A}^{(m\cdot)} + \mathbf{A}^{(\cdot\cdot)})/2$; for β_n, it is $(\mathbf{A}^{(\cdot n)} + \mathbf{A}^{(\cdot\cdot)})/2$; for $(\alpha\beta)_{mn}$, it is $(\mathbf{A}^{(mn)} + \mathbf{A}^{(\cdot\cdot)})/2$.

As in the random-effects case, it is possible to use matrices other than the mean as a reference matrix. In our example, instead of the overall mean, we use the summary matrix from the pooled data for $\mathbf{A}^{(\cdot\cdot)}$. To be consistent, we should also have used pooled data for the plot means $\mathbf{A}^{(m\cdot)}$ and the year means $\mathbf{A}^{(\cdot n)}$. We did not have the data accessible in this format at the time of these analyses, so we did not do this. Thus, we present the analysis with the cautionary note that our reference matrices are slightly inconsistent, but we are reasonably confident that this does not have a large effect on the qualitative results.

The decomposition analysis (eqs. 13–15) gives the contribution of each matrix entry to each treatment effect (i.e., to each plot effect, to each year effect, and to each plot-by-year interaction effect). It would be nice to have some way to compute a single number that measures the overall contribution of each matrix entry to each treatment factor. Some matrix entries are unaffected by the treatment and make a zero contribution to each level of the treatment. Others make small positive contributions at some levels and small negative contributions at other levels. The important matrix entries are those with large positive contributions at some treatment levels and large negative contributions at others. Taking the means of these contributions over the different levels of the factor does not work, because it is always approximately zero, just as in an analysis of variance the mean of the treatment effects is (exactly) zero.

This suggests using the variance, or perhaps the mean of the absolute values, of the contributions as a summary measure. In this chapter we use the means of the absolute values. This calculation is useful in simplifying the results of complex data sets with many levels of cross-classified factors. In our system, with 4 plots, 4 years, and 16 plot-year combinations (see below), taking these means yields a graph with a single line for the plot effects, a single line for the year effects, and a single line for the interaction effects. However, this simplification comes at a cost: presenting the results in this form obscures the contributions to the treatment and interaction effects, which are the original goal of the design (for complete factorial analyses, see Caswell 1989*a*; Walls et al. 1991).

TABLE 1. *Variance of λ among 16 Matrices for* Calathea ovandensis

Approximation	Equation	Value
Variance from mean	standard	0.0182
Variance from pooled	16	0.0187
Covariance approximation	5	0.0317
Variance approximation	7	0.0196

3 An Example: *Calathea ovandensis*

We now apply the analyses described above to a set of 16 matrices (four plots over four years) generated from a five-year study of a Neotropical understory herb, *Calathea ovandensis*. The life cycle was divided into eight stages: seeds, three vegetative stages (seedling, juvenile, and pre-reproductive) and small, medium, large, and extra-large reproductive plants. *C. ovandensis* has long-term seed dormancy. Seedlings have the highest mortality of all stages, and reproductives have low mortality. Plants that do not die sometimes shrink, sometimes remain the same size (stasis), and sometimes increase in size between seasons. Fertility is positively correlated with size (Horvitz & Schemske 1995).

Significant spatiotemporal variability is found in the vital rates and in the sensitivity structure (Horvitz & Schemske 1995). The population growth rates of the 16 plot-year matrices varied from 0.7356 to 1.2477, with an arithmetic mean of 0.9695 and a variance $V(\lambda) = 0.0182$ (Table 1). Nevertheless, the overall dynamics are well represented by a summary matrix $\mathbf{A}^{(\cdot\cdot)}$ that pooled all observations over the five-year period (Fig. 1). The dominant eigenvalue of this matrix is $\lambda^{(\cdot\cdot)} = 0.9923$ (Horvitz & Schemske 1995).

We characterize the variability in the population growth rate by the mean-squared deviation around the growth rate of the summary matrix, rather than as the variance around the mean. Let $\lambda^{(mn)}$ denote the growth rate in plot m in year n. Then, our measure of variability is

$$V_s(\lambda) = \sum(\lambda^{(mn)} - \lambda^{(\cdot\cdot)})^2/16\,. \tag{16}$$

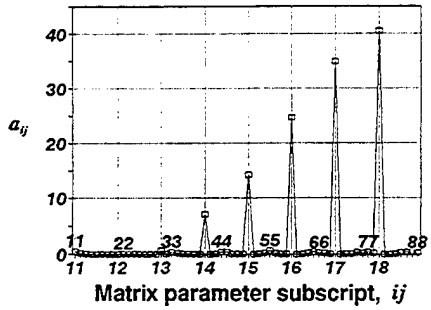

FIGURE 1. *Entries a_{ij} of the pooled summary matrix (Horvitz & Schemske 1995) for* Calathea ovandensis. *The 64 entries of the* 8×8 *matrix are arranged in column order: fates of seeds $(a_{11}, \ldots, a_{81})$, fates of seedlings $(a_{12}, \ldots, a_{82})$, and so on. Subscripts for the entries of the first row appear on the abscissa; subscripts for the diagonal elements appear directly above the matrix entry.*

The variance from the summary matrix calculated in this way is $V_s(\lambda) = 0.0187$ (Table 1).

Prospective Analyses

The sensitivities and elasticities of the summary matrix are shown in Figure 2. The largest sensitivities are s_{81}, s_{71}, s_{61}, and s_{51}, in that order. Additive perturbations thus exert the biggest effects if they occur in the vital rates that represent extremely rapid growth of newly germinated seedlings. Sensitivities to other seed transitions (s_{41} and s_{31}) and to the rapid growth of established seedlings (s_{82}, s_{72}, s_{62}, s_{52} and s_{42}) are also high. Within each stage, stasis and growth have higher sensitivities than fecundity.

The largest elasticity is e_{55} (stasis of small reproductives), followed by e_{54} (growth of pre-reproductives), e_{44} (stasis of pre-reproductives), and e_{11} (seed dormancy). Thus, proportional perturbations have the biggest impact if they affect the stasis of, and growth to, small reproductives.

There is little correlation between the sensitivity and the elasticity patterns (Fig. 2). This is not unusual; the effects of additive

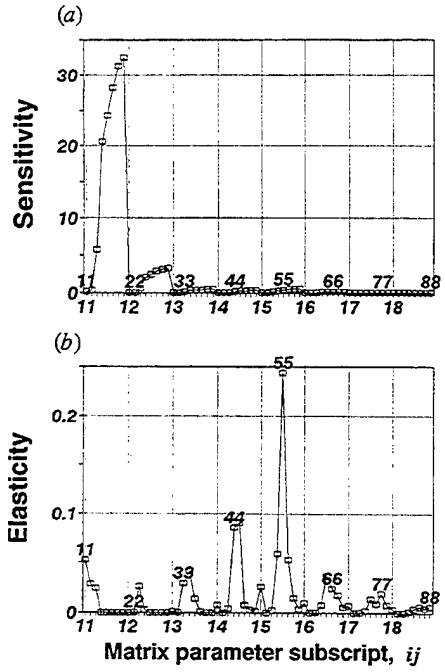

FIGURE 2. (a) *Sensitivities (s_{ij}) of λ to the corresponding entries of the pooled summary matrix.* (b) *Elasticities (e_{ij}) of λ to the corresponding entries of the pooled summary matrix. Axis labels as in Figure 1.*

and proportional perturbations are likely to differ.

Retrospective Analyses: Random Effects

The covariances of the matrix entries are shown in Figure 3*a*. The large positive values dominating the figure are covariances among the fecundities; a year or plot that is good for the reproduction of one size class tends to be good for the reproduction of all. The entries on the diagonal of this surface are the variances; these are

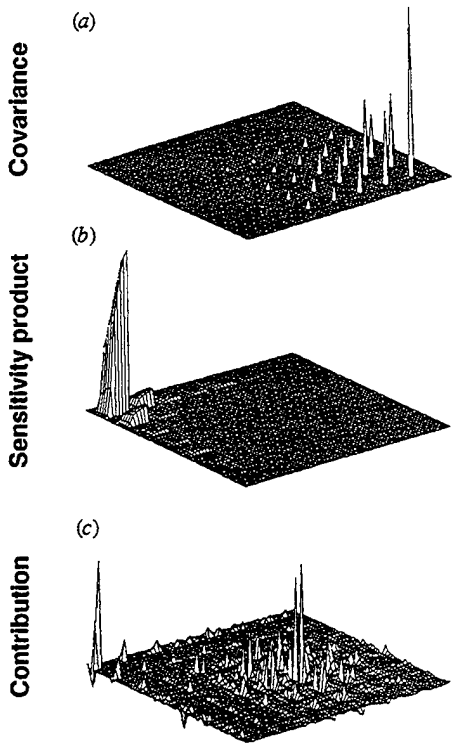

FIGURE 3. (a) *Covariances of the matrix elements* a_{ij} *and* $a_{k\ell}$ *over 16 plot-year combinations. Variances appear on the diagonal.* (b) *The products* $s_{ij}s_{k\ell}$ *of pairs of sensitivities, calculated from the pooled summary matrix.* (c) *Contributions of each pair of matrix entries to* $V_s(\lambda)$*, from the product of the corresponding elements in* (a) *and* (b)*. The order of the matrix elements in all three surfaces is the same as the abscissa in Figure 1.*

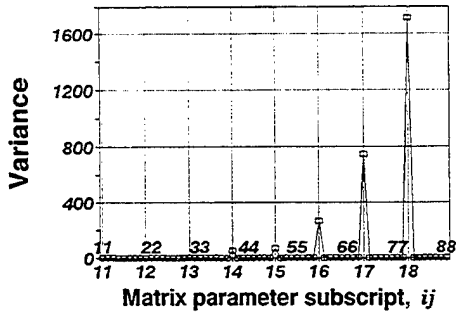

FIGURE 4. *The variances of the matrix elements a_{ij} over 16 plot-year combinations. Axis labels as in Figure 1.*

plotted in Figure 4. The variances of fecundities dwarf all the other variances.

The products $s_{ij}s_{k\ell}$ of pairs of sensitivities are highest for the germination and rapid growth of seeds (Fig. 3*b*). Thus, in this data set there is a negative correlation between the sensitivity of λ to a matrix entry and the variability in that matrix entry. The contributions to $V_s(\lambda)$ from each of the covariances is given by the element-wise product of Figures 3*a*,*b*; the result is shown in Figure 3*c*. Several large contributions from variance terms appear on the diagonal, and there are many small but not negligible contributions, both positive and negative, from the off-diagonal covariance terms. The sum of these values, as in equation (5), is 0.0317.

Taking sums across the rows (or down the columns) of the surface in Figure 3*c* gives the contributions χ_{ij} by the covariance method (eq. 6). The results are shown in Figure 5. This shows how $V_s(\lambda)$ is increased by positive covariances (including variances) of matrix entries and reduced by negative covariances among matrix entries. The largest of these contributions are from a_{65} (growth of small reproductives), a_{54} (growth of pre-reproductives), a_{31} (rapid growth of newly germinated seeds), and a_{45} (a negative contribution from covariances involving the shrinking of small reproductives). Negative contributions are also made by covariances involving a_{44} and a_{55} (stasis of pre-reproductives and small reproductives).

Figure 3 shows that covariances among the matrix entries cannot be ignored in this data set. Nevertheless, Figure 5*b* shows the

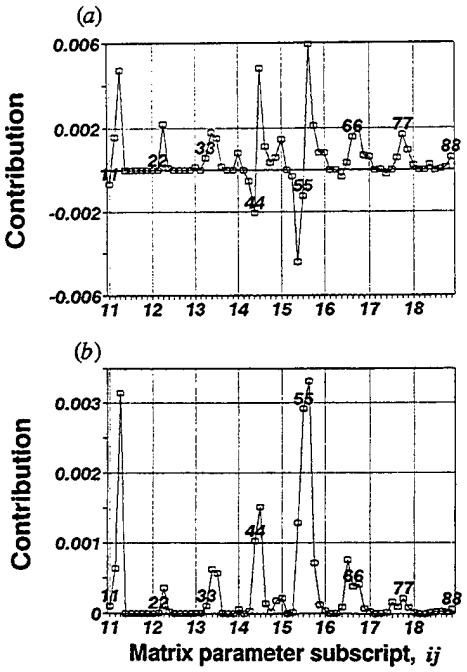

FIGURE 5. (a) *The total contribution (χ_{ij}) of matrix entry a_{ij} to the variance $V_s(\lambda)$, calculated by summing over the covariance contributions in Figure 3 according to equation (6).* (b) *The contributions (χ_{ij}^{ind}) of the variance of matrix entries to $V_s(\lambda)$ assuming that the matrix entries vary independently, as in equation (8). Axis labels as in Figure 1.*

contributions χ_{ij}^{ind} calculated using the variance method (eq. 8); these values are just the diagonal elements of Figure 3*c*. They sum to 0.0196 (Table 1).

The largest contributions to $V_s(\lambda)$ in this analysis are from the variances of a_{65} (growth of small reproductives), a_{31} (growth of newly germinated seeds), a_{55} (stasis of small reproductives), and a_{54} (growth of small reproductives). Note that ignoring covariances leads to the conclusion that the variance of a_{55} makes a large pos-

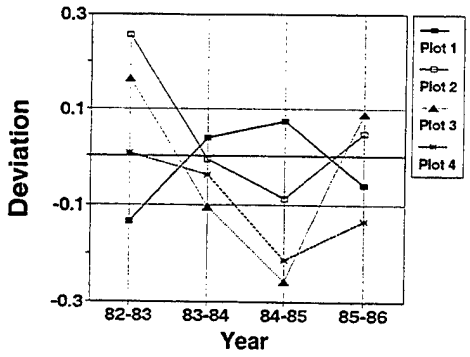

FIGURE 6. *Population growth λ for each plot in each year, expressed as a deviation from the growth rate of the pooled summary matrix.*

itive contribution to $V_s(\lambda)$; in fact, the covariances involving a_{55} make its net contribution to $V_s(\lambda)$ negative (Fig. 5*b*).

Retrospective Analyses: Fixed Treatments

Using the fixed-effect factorial design, we can break down contributions to variability in λ further, into independent effects of plots, years, and their interaction. Population growth rate is shown in Figure 6 as a function of plot and year. The plot and year effects α_m and β_n are shown in Figures 7*a*,*b*. Plot 2 had the largest positive effect on λ, and plot 4 the largest negative effect. Year 1982–83 had the largest positive effect, and 1984–85 the largest negative effect. The plot and year effects are of similar magnitude, although years are slightly more influential than plots. The temporal pattern differed among plots (Fig. 6), suggesting a plot-by-year interaction, which appears in the interaction effects $(\alpha\beta)_{mn}$ in Figure 7*c*.

We do not show the decomposition of each of the plot, year, and interaction effects into contributions from each of the matrix entries. Instead, we show the means of the absolute values of the contributions of each matrix entry to the plot effects, to the year effects, and to the interaction effects (Fig. 8).

The matrix entries most influential in determining plot effects are a_{65} (growth of small reproductives), a_{44} (stasis of pre-reproductives), a_{31} (germination and growth of seeds), and a_{45} (shrinkage of small reproductives) (Fig. 8*a*).

The entries most influential in determining year effects are a_{55}

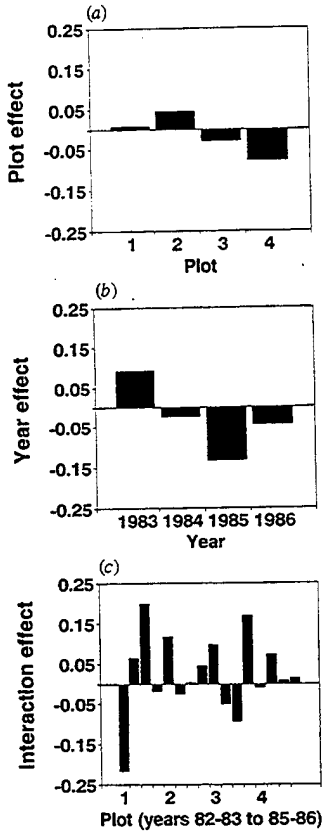

FIGURE 7. (a) *The main effects* α_m, $m = 1, \ldots, 4$, *of plots, calculated from equation (13).* (b) *The main effects* β_n, $n = 1, \ldots, 4$, *of years, calculated from equation (14).* (c) *The interaction effects* $(\alpha\beta)_{mn}$, *calculated from equation (15). Years, from 1982 to 1985, are shown within each plot.*

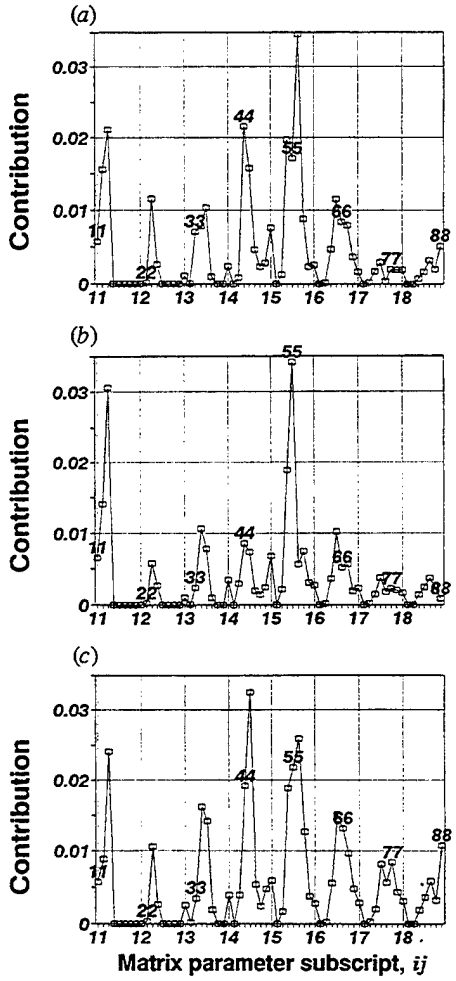

FIGURE 8. (a) *The mean, over 4 plots, of the absolute value of the contributions of each matrix element to the plot effect.* (b) *The mean, over 4 years, of the absolute value of the contributions of each matrix element to the year effect.* (c) *The mean, over 16 plot-year combinations, of the absolute values of the contributions of each matrix element to the plot-by-year interaction effect. Axis labels as in Figure 1.*

(stasis of small reproductives), a_{31} (germination and growth of seeds), a_{45} (regression of small reproductives), and a_{21} (seed germination) (Fig. 8*b*).

The matrix entries with the largest influence on interaction effects are a_{45} (growth of pre-reproductives), a_{65} (growth of small reproductives), a_{31} (germination and growth of seeds), and a_{55} (stasis of small reproductives) (Fig. 8*c*).

4 Discussion

We show computations of seven different measures of the "importance" of individual matrix entries to population growth: two prospective and five retrospective. Here we discuss the matrix elements that rank among the top four in each type of analysis (Table 2). We also examine the correlations among the seven measures of importance (Table 3).

The sensitivity and elasticity analyses pick out completely different sets of matrix entries as the most important. Additive perturbations of the matrix elements in the last four locations of the first column, representing extremely rapid growth of newly germinated seedlings, have the biggest effect on λ. Proportional perturbations, in contrast, have the biggest impact when they involve the stasis and growth of pre-reproductive and small reproductive plants, or seed dormancy. Sensitivity is weakly, but negatively, correlated with indices generated by the other approaches (Table 3), in spite of the fact that sensitivity appears in the calculation of all the other indices. This correlation would change if it was calculated using only the sensitivities of the nonzero matrix entries, that is, those that are free to vary. The largest such sensitivity is s_{31}, and we note that a_{31} also appears among the four most important entries in all five retrospective analyses.

Of the 64 matrix entries, only eight (a_{55}, a_{54}, a_{44}, a_{11}, a_{65}, a_{31}, a_{45}, and a_{21}) appear among the top four in importance according to elasticity or any of the retrospective analyses. None is important by all criteria. The growth of newly germinated seedlings (a_{31}) is important by all five retrospective indices; it contributes significantly to variance (according to both the covariance and variance methods), and its contribution to plot, year, and plot-by-year interaction effects is also important.

Only two matrix entries (a_{55} and a_{65}, the stasis and growth of small reproductives) are important according to four indices. Entry a_{55} has high elasticity and makes a large contribution to $V_s(\lambda)$ by the variance method. It has an important contribution to the year

TABLE 2. *The Indices (i, j) of the Four Most Important Matrix Entries*

	Method						
	Prospective		Retrospective				
			Random Effect		Fixed Effect		
Rank	Sensitivity	Elasticity	Covariance	Variance	Plot	Year	Plot-by-Year
1	8,1	5,5	6,5 (+)	6,5	6,5	5,5	5,4
2	7,1	5,4	5,4 (+)	3,1	4,4	3,1	6,5
3	6,1	4,4	3,1 (+)	5,5	3,1	4,5	3,1
4	5,1	1,1	4,5 (−)	5,4	4,5	2,1	5,5

NOTE.— Indices measured by two prospective and five retrospective methods. For the contributions to $V_s(\lambda)$ calculated according to the covariance method, the sign of the effect is also shown.

TABLE 3. *Correlations among the Two Prospective and Five Retrospective Measures of the Importance of the Matrix Entries to Population Growth*

	Prospective		Retrospective				
			Random Effects		Fixed Effects		
	Sensitivity	Elasticity	Variance	Covariance	Plot	Year	Plot-by-Year
Sensitivity	1.00	−0.13	−0.07	−0.08	−0.17	−0.13	−0.21
Elasticity	−0.13	1.00	0.01	0.71	0.63	0.76	0.69
Covariance	−0.07	0.01	1.00	0.46	0.41	0.14	0.47
Variance	−0.08	0.71	0.46	1.00	0.88	0.81	0.84
Plot effect	−0.17	0.64	0.41	0.88	1.00	0.71	0.89
Year effect	−0.13	0.76	0.14	0.81	0.71	1.00	0.74
Plot-by-year	−0.21	0.69	0.47	0.84	0.89	0.73	1.00

effect and to the plot-by-year interaction effect (Table 2). Entry a_{65} makes a large contribution to $V_s(\lambda)$ and to the plot and plot-by-year interaction effects.

Shrinkage of small reproductives (a_{45}) and the growth of pre-reproductives (a_{54}) are important according to three of the indices. Shrinkage of small reproductives has high elasticity and makes important contributions to $V_s(\lambda)$ by the variance method and to the plot-by-year interaction. The growth of pre-reproductives makes an important contribution to $V_s(\lambda)$ and to the plot and year effects.

Stasis of pre-reproductives (a_{44}) has high elasticity and makes an important contribution to the plot effect. Seed dormancy and seed germination (a_{11} and a_{21}) have high elasticity and make an important contribution to the year effect, respectively.

Table 3 shows the correlations between the various measures of "importance," underscoring the different insights produced by each analysis. Sensitivity and elasticity are nearly independent of contributions to $V_s(\lambda)$ calculated using equations (5) and (6), the appropriate variance decomposition for this data set (correlation coefficients -0.07 and 0.01, respectively). Thus, treating the 16 matrices as a random sample characterized by the variance of λ, the prospective and retrospective analyses clearly address different questions. Elasticity, however, is positively correlated with contributions to $V_s(\lambda)$ by the variance method.

Sensitivity is negatively correlated with the results of all the other analyses. Elasticity has positive correlations with most other analyses, and large ones with the plot (0.64), year (0.77), and plot-by-year interaction (0.69) effects.

The random- and fixed-effects analyses are positively correlated, but not always strongly. Contributions to $V_s(\lambda)$ from the covariance approach has correlations of 0.41, 0.14, and 0.47 with contributions to the plot, year, and plot-by-year interaction effects. Within the fixed-effect design, there are strong correlations between contributions to plot and year effects (0.72), plot and interaction effects (0.89), and year and interaction effects (0.74). This suggests that the plot and year effects tended to be mediated by variation in the same set of vital rates (Table 2).

Finally, we note that χ_{ij}^{ind} is highly correlated with elasticity and with contributions to all three fixed effects. Thus, a random-effects, retrospective analysis that is inappropriate for this data set does a good job of predicting the results of both a fixed-effect, factorial, analysis and an elasticity analysis.

There is no single best method for determining the "importance"

of the vital rates. It is important to define more precisely what we mean by importance, and to address specific, well-posed questions, such as the following.

What are the relative sensitivities of λ to incremental changes in the vital rates?

What are the relative proportional sensitivities of λ to proportional changes in the vital rates?

Over an observed sample of environmental conditions, how do the variances of, and covariances among, the vital rates contribute to the variance of λ?

How much does each of the vital rates contribute to the observed effect on λ of each of a set of fixed treatments?

In the case analyzed here, the prospective elasticity analysis identifies one vital rate, seed dormancy, that is not important according to the retrospective methods. Similarly, the factorial analysis identifies seed germination as making an important contribution to year effects; this vital rate is not identified as important by any other method. Despite these differences, both the transition to and the fates of small reproductives are identified as key events for *Calathea ovandensis*, both in predicting the outcome of hypothetical perturbations and in explaining the observed variation in population growth rate.

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Literature Cited

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs* 52: 335–351.

Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74: 1444–1454.

Calvo, R. N. 1993. Evolutionary demography of orchids: Intensity and frequency of pollination and the cost of fruiting. *Ecology* 74: 1033–1042.

Calvo, R. N., and C. C. Horvitz. 1990. Pollinator limitation, cost of reproduction, and fitness in plants: A transition matrix demographic approach. *American Naturalist* 136: 499–516.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theoretical Population Biology* 14: 215–230.

———. 1985. The evolutionary demography of clonal reproduction. Pp. 187–224 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, eds., *Population Biology and Evolution of Clonal Organisms*. Yale University Press, New Haven, Conn.

———. 1986. Life cycle models for plants. *Lectures on Mathematics in the Life Sciences* 18: 171–233.

———. 1989*a*. The analysis of life table response experiments. I. Decomposition of treatment effects on population growth rate. *Ecological Modelling* 46: 221–237.

———. 1989*b*. *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer, Sunderland, Mass.

———. 1996*a*. Demography meets ecotoxicology: Untangling the population level effects of toxic substances. Pp. 255–292 *in* M. C. Newman and C. H. Jagoe, eds., *Ecotoxicology: A Hierarchical Treatment*. Lewis, Boca Raton, Fla.

———. 1996*b*. Second derivatives of population growth rate: Calculation and applications. *Ecology* 77: 870–879.

———. In press. Analysis of life table response experiments. II. Alternative parameterizations for size- and stage-structured models. *Ecological Modelling*.

Caswell, H., and P. A. Werner. 1978. Transient behavior and life history analysis of teasel (*Dipsacus sylvestris* Huds.). *Ecology* 59: 53–66.

Caswell, H., R. J. Naiman, and R. Morin. 1984. Evaluating the consequences of reproduction in complex salmonid life cycles. *Aquaculture* 43: 123–134.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68: 1412–1423.

de Kroon, H. J., A. Plaiser, J. van Groenendael, and H. Caswell. 1986. Elasticity: The relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427–1431.

Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave desert. *Ecological Applications* 4: 446–460.

Heppell, S. S., J. R. Walters, and L. B. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: A modeling approach. *Journal of Wildlife Management* 58: 479–487.

Horvitz, C. C., and D. W. Schemske. 1986. Seed dispersal and environmental heterogeneity in a Neotropical herb: A model of population and patch dynamics. Pp. 169–186 *in* A. Estrada and T. Fleming, eds., *Frugivores and Seed Dispersal.* Junk, Dordrecht, The Netherlands.

———. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: Projection matrix analysis. *Ecological Monographs* 65: 155–192.

Kalisz, S., and M. A. McPeek. 1992. Demography of an age-structured annual: Resampled projection matrices, elasticity analyses and seed bank effects. *Ecology* 73: 1082–1093.

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75: 601–607.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.

Levin, L. A., H. Caswell, K. D. DePatra, and E. L. Creed. 1987. Demographic consequences of larval development mode: Planktotrophy vs. lecithotrophy in *Streblospio benedicti. Ecology* 68: 1877–1886.

Levin, L., H. Caswell, T. Bridges, D. Cabrera, G. Plaia, and C. DiBacco. In press. Demographic responses of estuarine polychaetes to sewage, algal, and hydrocarbon additions: Life table response experiments. *Ecological Applications.*

Lewontin, R. C. 1974. The analysis of variance and the analysis of causes. *American Journal of Human Genetics* 26: 400–411.

Martinez, M., and E. Alvarez-Bullya. 1986. Seed dispersal, gap dynamics and tree recruitment: The case of *Cecropia obtusifolia* at Los Tuxtlas, Mexico. Pp. 333–346 *in* A. Estrada and T. Fleming, eds., *Frugivores and Seed Dispersal.* Junk, Dordercht, The Netherlands.

Menges, E. S. 1990. Population viability analysis for an endangered plant. *Conservation Biology* 4: 52–62.

Mesterton-Gibbons, M. 1993. Why demographic elasticities sum to one: A postscript to de Kroon et al. *Ecology* 74: 2467–2468.

Phillips, P. C., and S. J. Arnold. 1989. Visualizing multivariate selection. *Evolution* 43: 1209–1222.

Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, and J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75: 584–606.

Sibly, R. M. 1996. Effects of pollutants on individual life histories and population growth rates. Pp. 197–224 *in* M. C. Newman and C. H. Jagoe, eds. *Ecotoxicology: A Hierarchical Treatment.* Lewis, Boca Raton, Fla.

van Groenendael, J., H. de Kroon, S. Kalisz, and S. Tuljapurkar. 1994. Loop analysis: Evaluating life history pathways in population projection matrices. *Ecology* 75: 2410–2415.

Walls, M., H. Caswell, and M. Ketola. 1991. Demographic costs of *Chaoborus*-induced defenses in *Daphnia pulex. Oecologia* 87: 43–50.